

EXOSKELETON, MOULT STAGE, APPENDAGE MORPHOLOGY, AND HABITS OF THE MIDDLE CAMBRIAN TRILOBITE *OLENOIDES SERRATUS*

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ABSTRACT. The external surface and morphology of the exoskeleton of *Olenoides serratus* is described; the exoskeletal layer has been replaced by illite and chlorite. The pleura curves down distally, there is no fulcral process or socket, but a flange assists in articulation. An early moult stage has the exoskeleton unmineralized and wrinkled, and was described as *Nathorstia transitans*. The type is redescribed; a second specimen is of the exoskeleton only. A new reconstruction of the biramous appendage is given. The outer branch was attached to the coxa so that it was extended close below the ventral cuticle of the body; the function was probably respiratory. The inner and ventral surfaces of the coxa, and the ventral side of the outer branch, were spinose. These limbs were adapted to seize soft prey, squeeze, and shred it, and pass it forward to the mouth; a manner in which these activities could have been effected is outlined. The probable musculature of the limbs and a possible gait are described; this gait is unlike other modes of progression in trilobites that have been proposed. How *O. serratus* may have jumped off the bottom and drifted is suggested, the swimming powers were probably feeble, it could have ploughed shallowly in soft sediment. By alternate flexure and extension of pairs of limbs it could have dug in search of prey or for concealment; a *Rusophycus* type of trace may have resulted from such activity. *O. serratus* is thus considered to have been a benthonic predator and scavenger. No plausible limb movements by which it could have made a *Cruziana*-like trace are evident; how this trace was made is an unsolved problem.

THE earlier description of appendage-bearing specimens of *Olenoides serratus* (Whittington 1975) included a new reconstruction of the animal and a brief discussion of habits. Here additional details of exoskeletal composition and morphology are given, including those of unusual articulating devices in the thorax. The rare early moult stage (*Nathorstia transitans*) is also redescribed. Further preparation, new photographs, and drawings have enabled a more detailed restoration of the biramous appendage. The limbs of *O. serratus* are now better known than those of any other species, and the basic limb movements here portrayed are those regarded as plausible by Manton (1977, pp. 39-53). Certain of these activities produce characteristic trackways. Studies of trace fossils attributed to trilobites (Bergström 1973; Birkenmajer and Bruton 1971; Campbell 1975; Crimes 1970, 1975; Martinsson 1965; Osgood 1970, 1975; Seilacher 1955, 1959, 1962, 1970) are largely concerned not with such relatively simple tracks but other and more complicated ones. These trace fossils have had to be interpreted in the absence of any incontrovertible evidence as to what animal made them, but suggestions have been derived from them of the behaviour and limb movements of trilobites. Certain of these suggestions are examined here with reference to *O. serratus*, and against the background of Manton's work. In *O. serratus* it appears that the filaments of the outer branch of the appendage cannot have been used in excavating or brushing away sediment, i.e. cannot have produced the fine scratches attributed to such an activity. Much attention has been devoted to the trace fossils *Rusophycus* and *Cruziana*. It appears plausible (text-fig. 14) that *O. serratus* could have made the former type of trace. On the other hand, no plausible solution has been advanced for the problem of by what limb movements was the trace fossil *Cruziana* made. I cannot devise one, and can see no plausible activity of *O. serratus* that would have resulted in this type of trace. No attempt is made here to re-assess any trace fossil. The suggestions made do, however, call into question interpretations of trace fossils that have gained some acceptance; greater caution is needed in such

interpretations. *O serratus* belongs to a relatively small Middle Cambrian group that had few thoracic segments and the cephalon and pygidium are of similar size. Caution must likewise be used in drawing generalizations from this single species.

LOCALITY AND STRATIGRAPHICAL HORIZON

Specimens referred to herein came from C. D. Walcott's 'Phyllopod bed' in the quarry that he opened in 1910 for collecting from the Burgess Shale. This quarry is situated on the ridge between Wapta Mountain and Mount Field, at an elevation of approximately 2286 m (7500 ft), 4.8 km (3 miles) north of Field, southern British Columbia, Canada. Fritz (1971) described the geological setting of the Shale, and showed that the quarry was within the *Pagetia bootes* faunule of the *Bathyriscus-Elrathina* Zone of the early Middle Cambrian. The Phyllopod bed is 2.3 m (7 ft 7 in.) thick, but the exact horizon from which Walcott's specimens came is not known. Parties led by the Geological Survey of Canada collected from the quarry in 1966 and 1967, and measured the levels within the Phyllopod bed from which their specimens were collected (Whittington 1971). In the explanations of the plates herein, specimens collected by Walcott, now in the U.S. National Museum, are recorded as from the Phyllopod bed. The level within this bed from which the Geological Survey of Canada's specimens came is given. Details of other specimens and their occurrence are in Whittington 1975, pp. 101-102, fig. 1.

METHODS AND SYMBOLS

Photographs. Those showing the exoskeleton (Pl. 17, figs. 1, 2; Pl. 18, figs. 1-3) have been taken using normal north-west lighting (north at the top of the plate), the specimen lightly coated with ammonium chloride sublimate. All other photographs were made on panchromatic film in ultraviolet radiation, after focusing in ordinary light. In some (Pl. 19, figs. 3, 4; Pl. 20, figs. 1, 3; Pl. 22, fig. 1) the radiation was directed at about 30° to the horizontal, the direction varied to bring out particular features. The direction is given in each explanation. In the remainder the radiation was directed at about 65° to the horizontal, and the specimen tilted to about 12°; this gives maximum reflection from the surface of the specimen. In all except Plate 22, fig. 3 (referred to as 'reflected'), the specimen was covered with a thin film of distilled water beneath a glass slip. The effect is to enhance definition and contrast between matrix and specimen; these photographs are referred to as 'under water'. The part of a specimen is taken to be that which shows the animal in dorsal aspect; photographs of a counterpart only are so specified in the explanations.

Text-figures. Two of the text-figures which explain my interpretation of the specimen are referred to as composite because they combine in one drawing, features shown by part and/or counterpart. Symbols used in the text-figures are as follows:

A, axis of promotor-remotor swing of coxa; ahr, articulating half-ring; am, anterior margin; an, antenna; ap, appendage; ax, axial ring; cb, coxa-body junction; ce, cercus; cox, coxa; d, depressor muscle; dl, distal lobe of gill branch; do, doublure; ex, dorsal exoskeleton; f, flexor muscle; fl, flange; fo, fold; g, suffix indicating gill (outer) branch; gn, gnathobase; gs, genal spine; G.S.C., Geological Survey of Canada; h, hinge joint; in, infilling; im, inner margin; iplf, interpleural furrow; is, inner surface; L, as prefix denoting left side of animal; le, levator muscle; ls, lateral spines; m, mould of exoskeleton; ma, margin; os, outer surface; p, pivot joint; pl, pleura; plf, pleural furrow; pls, pleural spine; py, pygidium, segments numbered 1py, 2py, etc.; pys, border spine of pygidium; pxl, proximal lobe of outer branch; R, as prefix denoting right side of animal; t, thorax, seven segments numbered 1t, 2t, etc.; U.S.N.M., United States National Museum (now National Museum of Natural History); v, ventral; ve, vein in rock; x, axis of articulation in thorax.

1-15, Arabic numerals used to denote successive thoracic segments, axial rings of pygidium, pleural furrows, podomeres of leg branch, etc. Also used to denote series of biramous appendages beginning with the most anterior shown by the specimen, when it was not the most anterior in the animal.

I-XV, Roman numerals used to denote successive biramous appendages in a series, beginning with the most anterior in relation to the animal, *not* the specimen.

Hachures represent minute scarps in the specimens, produced when the rock was originally split, or by preparation. The line runs along the upper edge of the scarp, the hachures directed down slope from this line. The scarps run along the broken edges of fragments of the exoskeletal layer, and at the changes in level which separate parts of the body. In the drawings they indicate the relative level of one part of the body to another.

Stipple indicates the position of ridges and furrows, other uses of stipple are explained individually.

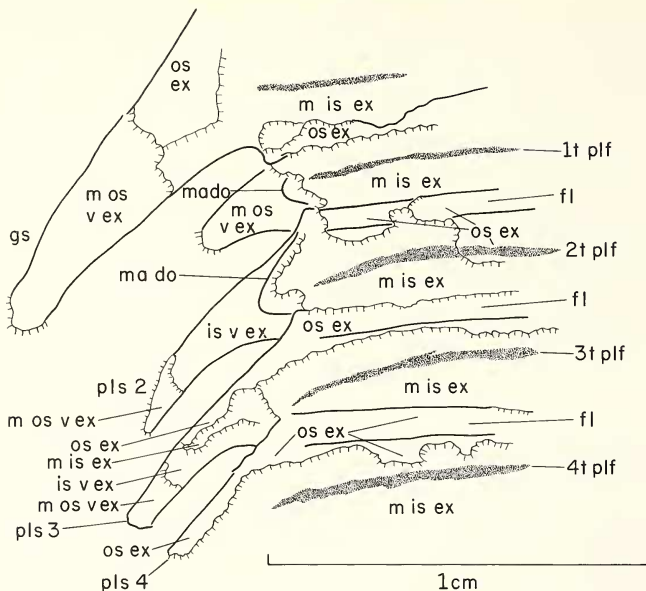
EXOSKELETON

The outer surface of the exoskeletal layer preserves in detail the original form (Pl. 17, fig. 1; Pl. 18, figs. 1-4). Granulation is coarsest on the posterior half of the axial rings, on the glabella and cheeks, and on the pleural ribs of thorax and pygidium; furrows are finely granulate to smooth. At the cephalic borders, and borders and spines of thorax and pygidium, the granulation grades into raised cusps which distally merge to form raised lines (Pl. 18, figs. 1, 4). On the anterior slope of the glabella and hypostome similar lines are formed (Whittington 1975, fig. 18, pl. 15, figs. 1-3). The steep scarp edges of the cusps face inwards, and so are opposed along the edges of the spines. On the ventral side of the spines and along the pygidial doublure are raised, anastomosing lines sub-parallel to the margin. The inner surface of the exoskeleton was smooth, as shown by the mould where the exoskeletal layer has been stripped off.

The broken edge of the exoskeletal layer (visible for example where it descends vertically into the doublure, Pl. 18, fig. 2, ex) appears black and shiny. A thin section was made across the posterior pygidial border of G.S.C. 61375, Walcott Quarry, level 6 ft 7.5 in. to 7 ft 3 in., an incomplete specimen showing portions of appendages. The exoskeletal layer is composed of minute flakes of a mineral, the flakes approximately at right angles to the surface. Electron microprobe analysis of the layer showed the presence of two distinct phases, an outer of illite (per cent by weight, MgO 4.85, Al_2O_3 31.32, SiO_2 37.20, S 0.18, K_2O 5.19, CaO 0.15, FeO 13.93, total 92.82, minus water), and an inner of chlorite (per cent by weight, MgO 9.93, Al_2O_3 24.08, SiO_2 25.51, S 0.08, K_2O 0.67, CaO 0.15, FeO 27.56, total 87.98, minus water). A fragment of the exoskeletal layer removed from G.S.C. 61374 (Pl. 18, fig. 3), gave the X-ray powder diffraction pattern of illite. It is assumed that the exoskeleton was originally mineralized with calcium carbonate, then replacement by illite group minerals occurred at some stage in diagenesis, perhaps at an early stage in an anoxic environment. Analyses quoted by Conway Morris (1977, p. 5) indicate that the soft parts of a fossil worm from the Burgess Shale are preserved in a film composed of calcium aluminosilicates, formed at some stage in diagenesis. Piper (1972, p. 173) remarked on the presence of diagenetic chlorite in portions of the Burgess Shale.

ARTICULATION OF THE THORAX

The earlier description of G.S.C. 34694 (Whittington 1975, pp. 119-120, pl. 20, figs. 1, 2, 4; pl. 21, figs. 1, 2; text-fig. 22) was primarily concerned with the appendages. Further preparation has revealed more completely the cheek (Pl. 18, fig. 4), and also the structure of the thoracic segments, including the articulating flange briefly alluded to earlier (Whittington 1975, p. 129). The flange fitted below the posterior pleural band of the segment in front, that of the first thoracic segment below the posterior border of the cephalon. Where the outer surface of the dorsal exoskeleton, or the mould of the inner surface, is not broken, the flange is concealed (e.g. right side of pleurae 5 to 7, Pl. 18, fig. 3; Whittington 1975, pl. 1, fig. 2; pl. 9, fig. 1). In 34694 the outer surface of the flange is exposed by the split or by preparation (Pl. 17, fig. 1; text-fig. 1; Pl. 18, fig. 2; text-fig. 2). The mould of the inner surface of the exoskeleton of the pleura, where exposed, lies only slightly above the outer surface of the exoskeleton of the succeeding flange, so that the two surfaces may in places appear to pass one into the other; in other places the slight difference in level is clear. The posterior margin of each flange is delineated by a narrow groove, and the flange is granulate. The flanges of the pygidium and seventh thoracic segment have been completely exposed by excavation (Pl. 18, fig. 2), in more anterior segments the flange is partially covered by the posterior pleural band. The abaxial margin is directed inwards and forwards, making a slight angle with the outer edge of the pleural spine. The flange is widest (exs.) abaxially, slightly narrower over most of its extent, proximally narrowing progressively as it curves down into the axial furrow. In the base of this furrow it merges into the outermost portion of the articulating half-ring. The ventral exoskeleton of the pleural spine extends inwards to form a band along the abaxial edge of the pleura, which narrows forwards and dies out, and does not extend under the flange. Postero-laterally the inner



TEXT-FIG. 1. Explanatory drawing of posterior portion of cheek lobe and pleural regions of first four thoracic segments in original of Plate 17, fig. 1.

EXPLANATION OF PLATE 17

Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

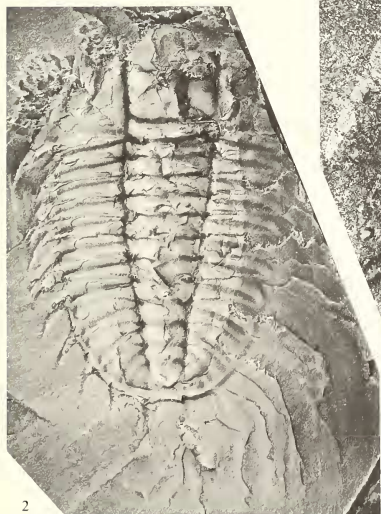
Fig. 1. G.S.C. 34694, level 6 ft 7.5 in. to 7 ft 3.5 in. Portions of posterior border of cephalon and thoracic segments 1-4, $\times 5$. For interpretation see text-fig. 1.

Fig. 2. G.S.C. 34694, level as fig. 1, entire, $\times 1.25$.

Fig. 3. U.S.N.M. 194000, under water, $\times 5$.



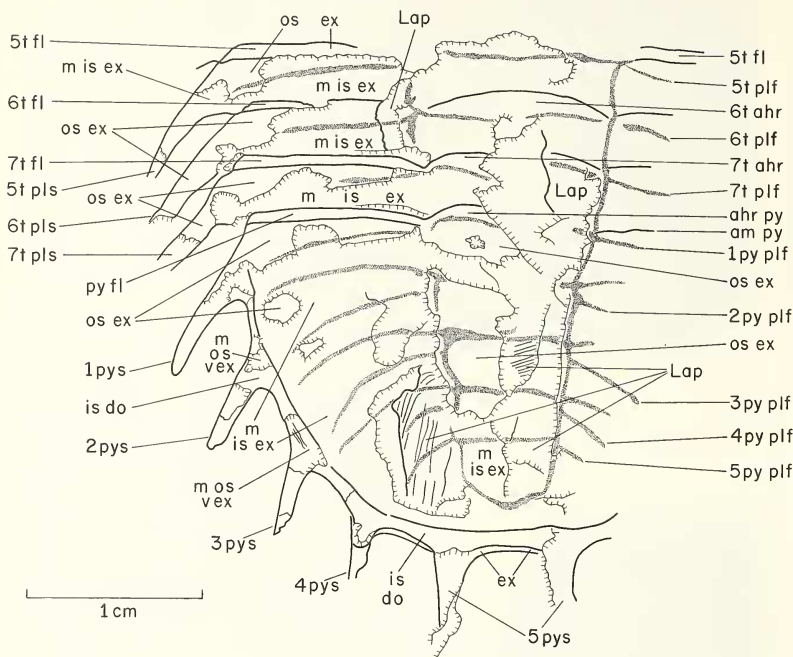
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TEXT-FIG. 2. Explanatory drawing of axial region and left pleural region of last three thoracic segments and pygidium of original of Plate 18, fig. 2.

EXPLANATION OF PLATE 18

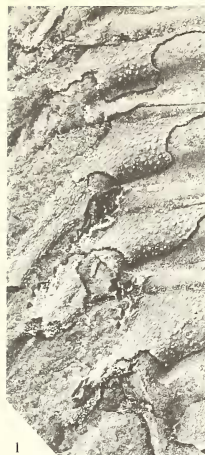
Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

Fig. 1. G.S.C. 34694, level 6 ft 7.5 in. to 7 ft 3.5 in. Distal portions of left thoracic pleurae 4-7 and the first pygidial pleura, showing details of external surface, $\times 5.5$.

Fig. 2. G.S.C. 34694, level as fig. 1. Portions of thoracic segments 4-7 and pygidium, $\times 4$. For interpretation see text-fig. 2.

Fig. 3. G.S.C. 61374, level 5 ft 5 in. to 6 ft 2 in. Right side of axial region of thoracic segments 1-7 and a portion of the pygidium, $\times 3$. Portions of right pleurae covered by a thin layer of shale, through which form of pleurae and pleural spines has been impressed by compaction.

Fig. 4. G.S.C. 34694, level as fig. 1, left half of glabella and portion of cheek lobe, $\times 4$. Fragments of exoskeletal layer showing external surface, adhere to anterior portion of glabella, palpebral lobe, and adjacent areas of cheek and border.



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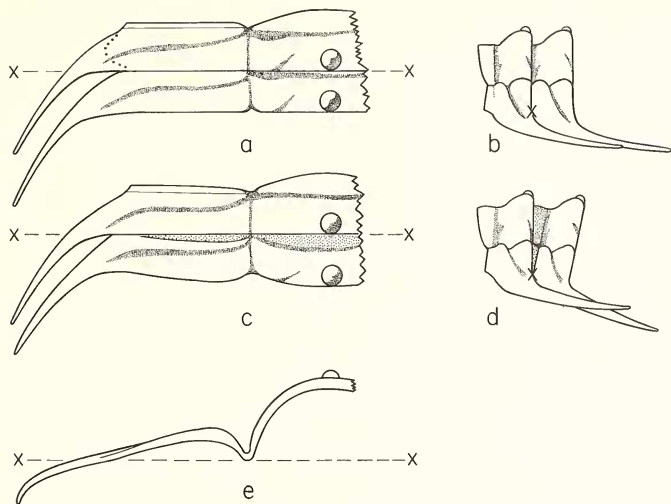


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margin of the doublure curves around to meet the posterior margin of the pleura a short distance inside the base of the pleural spine. The flange thus appears to have lain beneath the dorsal exoskeleton of the preceding pleura; only distally may it have passed beneath a narrow strip of doublure. The articulating half-ring is of length (sag.) about one-third that of the axial ring. A median posterior tubercle is present on each axial ring and the first four of the pygidium. Most specimens split to reveal the inner surface of the exoskeleton of the thoracic rings, the outer is rarely preserved. One exception (Pl. 18, fig. 3) has the median tubercle of the last thoracic segment prolonged into a short backwardly directed spine, possibly other thoracic median tubercles were similar; those of the pygidium are steep on the posterior side.

In preparing restorations of *Olenoides serratus* (Whittington 1975, p. 122) I made certain assumptions about original convexity of the exoskeleton. That of the pygidium was based on the pygidium of a different species illustrated by Fritz (1968, pl. 39, figs. 4, 5). I assumed that the inner portion of the thoracic pleura was horizontal, because the hinge between it and the next pleura must have run along it, and that the outer portion, the pleural spine, was probably directed gently downwards. It is difficult to assess from 34694 or other specimens the extent of the flattening that has taken place. Cracks and vertical displacement of parts are characteristic of the cephalon, and the hypostome is commonly pressed against the underside of the glabella (Pl. 17, fig. 2; Whittington 1975, pl. 1, figs. 2, 3). Axial rings of the thorax characteristically show a longitudinal zigzag crack, suggestive of the strong original convexity. The axial region of the pygidium is not so cracked, nor are the pleural regions of thorax and pygidium. There are longitudinal cracks in pleural spines, but not transverse fractures as might be expected if the spines had been steeply inclined. In the present restoration (text-fig. 3) the axial ring is accordingly strongly convex, the pleura (including the flange) is gently convex transversely, and the pleural spine is gently downwardly inclined. There is no evidence of geniculation at a fulcrum in the pleura, so I abandon my earlier view that the inner portion was horizontal, the outer flexed down. The position of the hinge line means that on flexure both articulating half-ring and flange would have moved back relative to the segment in front, covering the gap as it opened (text-fig. 3c, d). The axial furrow is shallow and broad between axial ring and posterior pleural band, but deepens as it descends to either margin. The narrow (exs.) band that connects flange and articulating half-ring shows no evidence of an axial process, so that I do not accept the view of Bergström (1973, p. 22) that such an articulating process is present. The antero-lateral angle of the flange is rounded, and affords no evidence of a fulcral process. Instead of such a process, the distal portion of the flange helped to maintain each pleura in the correct position relative to those adjacent. I consider it unlikely that the pleura sloped more steeply outwards than shown in text-fig. 3e, because this would have meant that the hinge line would have run below the level of the axial furrow, and that therefore on flexure a gap would have opened at this furrow as well as along the entire axial ring and adjacent portion of the pleura. Such a gap, on flexure of the amount shown in text-fig. 3c, d, would not have been bridged by the articulating half-ring and flange.

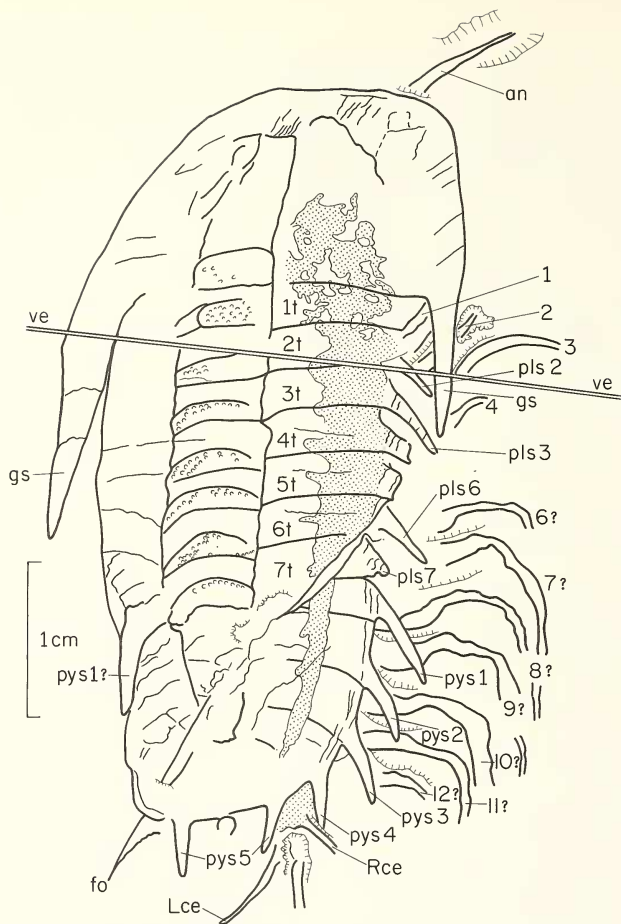
The morphology and manner of articulation of the thorax of *O. serratus* is in sharp contrast to that occurring in the Lower Cambrian *Crassifimbria walcotti* (Palmer 1958, pp. 159–160, text-fig. 5) and the Middle Cambrian *Bolaspidea houseensis* (Robison 1964, pl. 89, figs. 8, 9). In these species the inner portion of the pleura is horizontal, the outer part flexed down at the fulcrum, the hinge line lying along the straight edge of the inner portion; the outer portion is faceted, and Palmer describes the device which limits enrolment. This type of articulation is characteristic in post-Cambrian trilobites (Whittington and Evitt 1954, pp. 21–24), and may be aided by ball-and-socket joints. In *O. serratus* there is no clearly defined fulcrum, ball-and-socket joints do not appear to be developed, but the flange acts distally as a guide and medially as a protection during flexure. This situation is similar to that in redlichiids and olenellids (Öpik 1970, pp. 3–5; Bergström 1973, p. 17, pl. 2, fig. 4), in which the fulcrum was absent and the pleura curved down distally, each guided under the one in front during enrolment by an antero-lateral projection. The development of the broad flange in *O. serratus* is distinctive, indicative of the variety of modes of articulation in Cambrian trilobites.



TEXT-FIG. 3. Restoration of left halves of two mid-thoracic segments of *Olenoides serratus*, in extended (*a*, *b*) and flexed (*c*, *d*) positions, respectively dorsal and left lateral views. *e*, posterior view. × and dashed line indicate position of hinge line, coarse stipple on portions of flange and articulating half-ring exposed by flexure. Dotted line on left side of anterior segment in (*a*) indicates position of inner margin of doubleure.

THE NEWLY MOULTED EXOSKELETON, '*NATHORSTIA TRANSITANS* WALCOTT, 1912'

Henningsmoen (1975) remarked that if a newly moulted individual were preserved, it might well be wrinkled and deformed, and mistaken for a new species. This was the case with '*Nathorstia transitans*', a deformed specimen described as a new genus and species by Walcott (1912, pp. 191, 194-195, 216, pl. 28, fig. 2). In low-angle radiation (Pl. 19, figs. 3, 4) the specimen appears only slightly darker than the surrounding rock, and in contrast to specimens of *O. serratus* (Pl. 17, fig. 2) it shows little relief and the surface has a wrinkled appearance. There is no mineralized exoskeletal layer, the glabella in front of the occipital ring is defined only on the right side, and eye lobe, eye ridge, and facial suture cannot be seen, wrinkling being conspicuous on the cephalon. The rings of the axial region of thorax and pygidium are visible, the posterior portion of each thoracic ring showing a transverse granulated band. Interpleural furrows are best defined as narrow ridges on the counterpart (Pl. 19, fig. 4), pleural furrows can scarcely be detected. Preparation has revealed the genal spines, and in the counterpart (left side of Pl. 19, figs. 2, 4) right pleural spines 3 and 6, and right pygidial border spines 1-5. Portions of appendages appear as darker strips on the right side, outside and postero-lateral to the exoskeleton. Walcott's illustration was of the part only, photographed in a manner which reflected light from the specimen. In reflected radiation (Pl. 19, figs. 1, 2), part and counterpart show particularly clearly the appendages and genal and border spines. The part shows as a reflective area the trace of the alimentary canal, broadest anteriorly,



TEXT-FIG. 4. Composite explanatory drawing of U.S.N.M. 57685, cf. Plate 19, figs. 1-4. Stippled area is trace of alimentary canal.

EXPLANATION OF PLATE 19

Olenoides serratus (Rominger, 1887). U.S.N.M. 57685, holotype of *Nathorstia transitans* Walcott, 1912, Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia. For interpretation see text-fig. 4.

Figs. 1, 3. Original of Walcott, 1912, pl. 28, fig. 2, respectively under water, $\times 2$; west, $\times 1.5$.

Figs. 2, 4. Counterpart, respectively under water, $\times 2$; showing posterior portion of cephalon, thorax, pygidium, and portions of appendages, north-west, $\times 2$.



1



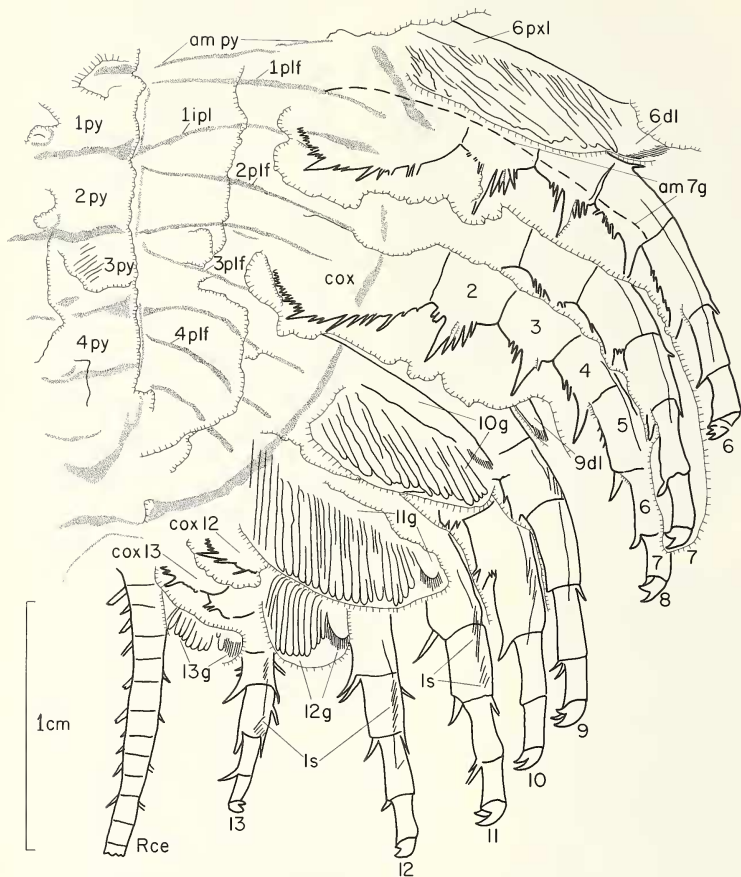
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TEXT-FIG. 5. Composite explanatory drawing of G.S.C. 34694, cf. Plate 20, figs. 1-4.

EXPLANATION OF PLATE 20

Olenoides serratus (Rominger, 1887). G.S.C. 34694, Phyllopod bed, level 6 ft 7.5 in. to 7 ft 3.5 in., Middle Cambrian, Burgess Shale, British Columbia. For interpretation see text-fig. 5.

Figs. 1, 2. Right half of pygidium and appendages, respectively north-west, under water, $\times 2.5$.

Figs. 3, 4. Counterpart, right half of pygidium and appendages, respectively south, under water, $\times 2.5$.



1



2



3



4

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medially and posteriorly having lobate projections which may be traces of proximal portions of diverticulae (text-fig. 4). In ordinary light portions of this area are stained yellow-brown.

My interpretation (text-fig. 4) differs from that of Walcott's (1912, pl. 28, fig. 2) retouched figure. He shows the right eye lobe as a strongly reflective crescent, but no such feature can be traced on part or counterpart (Pl. 19, figs. 1, 2). The antenna, poorly preserved leg branches, and cerci were shown by Walcott, but he labelled the left genal spine as a 'leg (mandible?)', and the proximal portions of pygidial border spines 2 and 3 as 'thoracic legs'. He considered that the proximal podomeres of the limbs were setose, but I cannot confirm this observation. He also mentions 'indications of a branchial lobe' in two other specimens, but no such specimens are preserved and labelled in his collections. He writes of the leg branches having been 'pushed out from beneath the dorsal shield'. It appears that the traces of both alimentary canal and appendages have been moved the same distance to the right relative to the exoskeleton. Such displacement is invariable in specimens of *O. serratus* (Whittington 1975, pp. 103-104, fig. 2).

Raymond (1920, p. 31) suggested that this specimen was a recently moulted *O. serratus* because of its appearance as a shadowy impression, and because the outline, position of eye lobe, pygidial spines, and presence of cerci, are all like that species. This opinion has been repeated (Størmer 1942, p. 147; Hupé in Piveteau 1953, p. 149; Harrington in Moore 1959, p. O76, O149), and is reinforced by this investigation. The size of the specimen, relative size of cephalon and pygidium, the thorax of seven segments, the shape, length, and direction of genal, pleural, and pygidial border spines, all agree to suggest that it should be assigned to *O. serratus* and not to any other species (see lists in Rasetti 1951, pp. 103-104; Fritz 1971, fig. 5) occurring at the same horizon. Simonetta and Delle Cave (1975, p. 6) questioned this identification because of the apparent absence of pleural spines, but this view is no longer tenable. It is typical of the way in which *O. serratus* is preserved in showing displacement of soft parts relative to the exoskeleton. Not only does the latter appear to be unmineralized, but the outline is asymmetrical, and pleural and pygidial spines are present on the right but not on the left side. These features are consistent with the carcass having been buried at an oblique angle to the bedding, tilted down to the left, and inclined forwards and downwards, and subsequently compressed (compare discussion of preservation of *Naraoia* in Whittington 1977, pp. 413-416, figs. 1, 3). To this attitude of burial may be related the direction of the wrinkling and fold in the specimen, the displacement of soft parts, and other features. The absence of traces of sutures is consistent with the supposed newly moulted condition of the animal.

The 1975 study was based on thirty examples of *O. serratus* (fifteen from the Walcott collection, U.S. National Museum) which had the appendages preserved and the exoskeleton mineralized; the range in exoskeletal length (sag.) lies between 5.2 and 8.1 cm (Whittington 1975, pp. 101-102, 128). The smallest specimen is thus only slightly longer than 57685 (length (sag.) 4.8 cm). An intensive search of the Walcott collection has revealed only one other (Pl. 17, fig. 3) example which lacks the mineralized exoskeletal layer with a length (sag.) of 2.2 cm. The exoskeleton is slightly distorted, preserved as a wrinkled, reflective film, showing no trace of appendages. It is exposed from the ventral side, and shows the narrow doublure of cephalon and pygidium, traversed by thin lines subparallel to the margins. Outline, relative size of cephalon and pygidium, seven thoracic segments, size, direction, and form of genal, pleural, and pygidial border spines are typical of

EXPLANATION OF PLATE 21

Olenoides serratus (Rominger, 1887). G.S.C. 34694, Phyllopod bed, level 6 ft 7.5 in. to 7 ft 3.5 in., Middle Cambrian, Burgess Shale, British Columbia. See text-fig. 5.

Fig. 1. Counterpart, details of right appendages 9-13 and cerci, under water, $\times 5$.

Fig. 2. Details of ventral and inner margins of coxae 6 and 8, ventral spines of podomere 2 of leg branch 8, under water, $\times 10$.

Fig. 3. Details of ventral margin of coxa 12, lamellae of gill branch 12, coxa and podomeres 2-5 of limb 13, under water, $\times 5$. To lower left is portion of left limb 11.

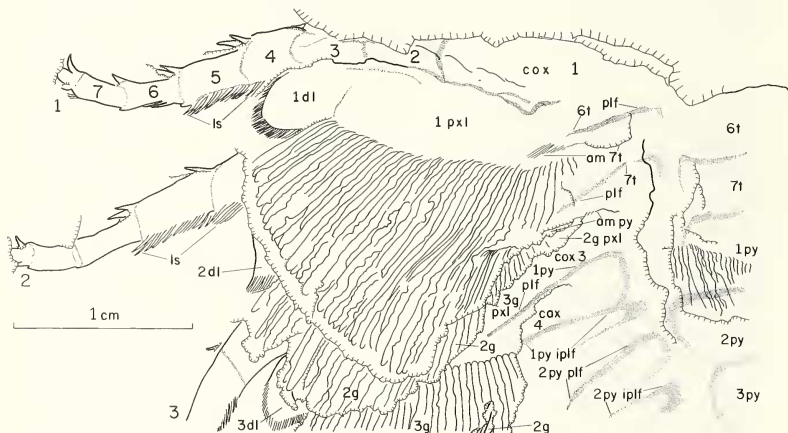


WHITTINGTON, *Olenoides*

O. serratus. It differs from Walcott's type in that the broad, parallel-sided glabella, extending forwards to the border furrow, is outlined. On the right cheek close to the mid-part of the glabella is a curved, reflective strip probably representing the eye lobe, and the course of the facial suture may be traced.

FUNCTIONAL MORPHOLOGY OF THE BIRAMOUS APPENDAGE

Morphology and attitude on burial. Two specimens have been prepared further and selected for re-illustration, not only because they show the morphology of the appendage in detail, but because they show two characteristic ways in which the branches are preserved. In text-fig. 5 (cf. Pl. 20, figs. 1-4) the successive coxae and leg branches are curved through 60° to 80° , and inclined backwards and downwards at a slight angle to the bedding plane, so that each passes below the one following. The inner margin shows rows and groups of spines, the outer a smoother curve showing rare small spines. Inside this outer margin in podomeres 4, 5, and the proximal portion of 6, is a narrow band along which oblique striations are rarely visible (Pl. 21, fig. 1). This band appears to be the trace of the lateral spines flattened against the surface. The outer branch lies on, and in leg branches 6-10 partly in front of, the leg branch, the lobate portion is narrow (exs.), the lamellae short and strongly outwardly directed. This appearance is in sharp contrast to that of the outer branch of appendage 1 in text-fig. 6 (cf. Pl. 22, figs. 1, 2), which lies behind the leg branch;



TEXT-FIG. 6. Explanatory drawing of portion of the counterpart of G.S.C. 34695, cf. Plate 22, figs. 1, 2.

EXPLANATION OF PLATE 22

Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

Figs. 1, 2. G.S.C. 34695, level 6 ft 11 in. to 7 ft 0 in., counterpart, respectively west, under water, $\times 3.3$.

For interpretation see text-fig. 6.

Fig. 3. G.S.C. 34697, level 6 ft 11 in. to 7 ft 2 in., gill branch and portion of leg branch of left side, showing fine hairs at tips of distal lamellae of gill branch, reflected, $\times 5$.



WHITTINGTON, *Olenoides*

the proximal and distal lobes are wide, the lamellae long and arranged fan-wise. The leg branch is extended in an 'S' curve, rows of fine spines extend from the margins of podomeres 4 and 5, and the distal claws are spread in a group of three, the median largest, not curved inwards in an overlapping group. In text-figs. 7, 8, I reconstruct the morphology of the appendage in a way that is consistent with explaining these different appearances as resulting from different attitudes on burial and the effect of compaction. In text-fig. 7, two appendages are shown in the burial position of 34694, the posterior side of the antero-posteriorly flattened coxa and leg branch towards the observer, the outer branch directed up towards the observer, and hence foreshortened. Compression vertical to the bedding plane would give the appearance seen in 34694, the outwardly directed spines on podomeres 4 and 5 of the leg branch being flattened against the wall of the podomere. Text-fig. 8 shows two appendages, viewed obliquely, in the burial position of 34695. Compression vertical to the plane of bedding would result in the outer branch lying undistorted, but coxa and leg branch being compressed obliquely (postero-ventrally). Thus the ventral spines of podomeres 4 to 6 came to lie on one side of the leg, the row of lateral spines on podomeres 4 and 5 form a row on the opposite side, and the terminal claws are divergent. Text-figs. 7, 8 show the spines of the coxa, and ventral spines of podomeres 2-6, in more detail than the 1975 reconstructions. The lateral spines of podomeres 4-6 are termed spines rather than setae because of the tapering, thorn-like form. They arise from the probably curved antero-dorsal and postero-dorsal surfaces of the podomeres; the rare spines on the dorsal side of the leg (Pl. 21, fig. 1) may be lateral spines displaced during burial.

Other examples of the two kinds of preservation discussed above are shown by the specimens previously described. In numbers 58588A, 58588B, 58589 (left limbs 5-7), and 65514 (right appendages 3-6), illustrated in Whittington 1975, pls. 2, 4, 5, 10, the appearance is like that of appendages 6-8 of 34694. The attitude seen in appendages 1-3 of 34695 is displayed by appendages of 65513, left 8-15 of 65514, and those of the right side of 34697 (Whittington 1975, pls. 7, 10, 24). As might be expected, not all specimens fit into these categories, or even intermediates between them, because of the varied attitudes on burial. The two examples selected here show the following features of preservation that are common to all specimens of *O. serratus* which have a mineralized exoskeleton and show traces of appendages (Whittington 1975, pp. 102-104, 127):

(i) The appendages are in an original serial relationship to each other, but displaced relative to the exoskeleton. In each example the coxae lie beneath the pleural region, beneath the outermost portion in 34694.

(ii) Successive branches in a series are imbricated, the lamellae of the outer branch extending backwards dorsal to the one following, each leg passing below (ventral to) the one following. A thin layer of rock separates successive branches, and the branches from the exoskeleton. These rock layers are shown by the minute scarps that intervene between successive branches. The scarps were produced when the rock was split, or by preparation, and are shown by hachures in the text-figures.

(iii) Leg branch and outer branch extend out in the same direction from the coxa, are not divergent, and are not disposed at varying angles to each other.

(iv) The body has been compressed, so that while the exoskeleton shows relief (reduced from the original) the appendages are preserved as an extremely thin layer, darker than the shale, and reflective; the reflectivity varies from specimen to specimen. Furrows and ridges in the exoskeleton have been impressed on to the appendages.

Function of outer branch. The four features of preservation discussed above imply that:

(a) the long lamellae of the outer branch were extended backwards and slightly upwards in life, over the next one or two succeeding appendages (Whittington 1975, fig. 27). The outer branch and leg branch are never preserved in an alternating, imbricated series, as they might have been if the outer branch had been rotated so that the lamellae were downwardly directed. The length of the lamellae, and their apparent stiffness (apparent because in any one branch they are preserved

subparallel, rarely displaced), appears to have precluded their being swung down between successive limbs.

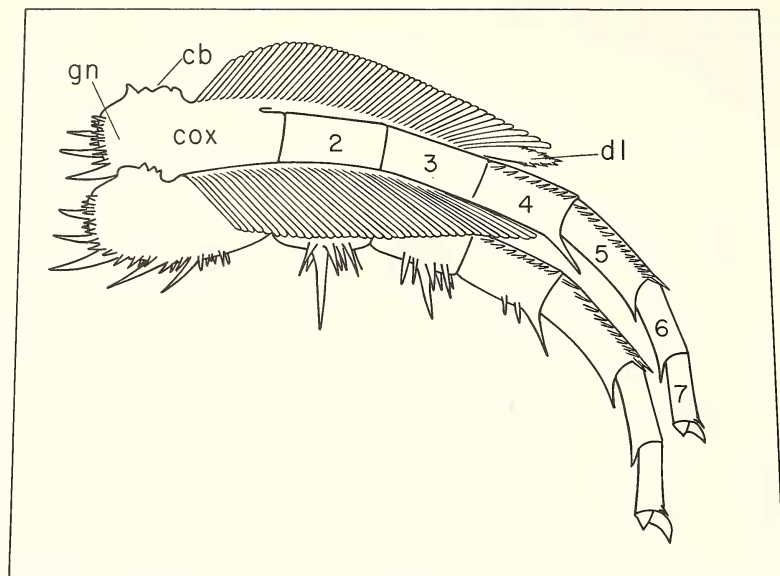
(b) proximally the outer branch was attached to the inner, postero-dorsal edge of the coxa, adjacent to the coxa-body junction (text-fig. 6). The distinctive way in which each series of branches is preserved, and the attitude in which the two branches appear to have been buried (text-figs. 7, 8), implies that this attachment was relatively rigid. There is no evidence that the outer branch could rotate or swing to and fro about the junction with the coxa.

These implications mean that the outer branches of the appendages in *O. serratus* were imbricated close beneath the ventral cuticle of the pleural regions, and cannot have been used to rake the sediment surface. Their position does not encourage the view that food particles were trapped by the lamellae. There seems no arrangement by which such particles could have been scraped off, collected, and conveyed to the mouth. The lamellae are preserved as long, flat strips, imbricated, the edge nearer the observer ragged as a result of breakage (Pl. 22, figs. 1, 2). The tip of each lamella is rounded and bears a few, fine setae (Pl. 22, fig. 3). The lamellae may have had the form of long, thin slats (Whittington 1975, p. 127).

A rough calculation, based on my restoration (1975, fig. 25) suggests that the combined areas of the outer surfaces of the filaments of the limb series was three times that of the ventral integument of the pleural regions. This integument is known only from the dark area in the centre of the appendages in 34692 (Whittington 1975, fig. 20; pl. 17, fig. 1), which reveals nothing of its structure. Oxygen could have been absorbed through it; whether or not it bore special gill structures (Bergström 1969, pp. 410-411) is unknown. I conclude that the primary function of the outer branches of the appendages in *O. serratus* was in respiration, and that the animal was not a filter feeder.

A more difficult question is on the possible function of the gill branch in swimming (Whittington 1975, p. 132, fig. 30). Once launched off the bottom (see next section) the coxae and leg branches would have to have been swung back into a trailing position to lessen their resistance to forward progress. If the junction between outer branch and coxae was relatively rigid, as implied above, the outer branch would have been pressed against the ventral cuticle, to an amount dependent upon the flexibility of the long lamellae. Only intrinsic musculature within the lobate portion of the outer branch could have enabled the outer branch to have been moved away from the ventral cuticle and back, to suck in and expel water and create a current that might have aided swimming. Whether such musculature was present is unknown, and the swimming powers of *O. serratus*, which may have been caused by such movements in a metachronal rhythm, are uncertain. Perhaps *O. serratus* had little or no swimming ability.

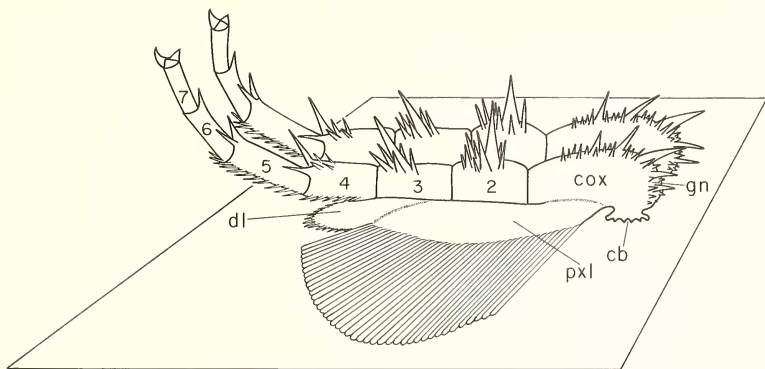
Outer branch of other species. The nature of this branch is not as well known in other species. For example, the basis for the reconstruction by Cisne (1975, figs. 1-3, pp. 47, 53-54) of the exite of *Triarthrus eatoni* has not been fully documented, but he shows the series as imbricated in the same sense as in *O. serratus*, and remarks that it was 'rather stiff and rigidly attached to the coxa'. Bergström's views on the nature and function of the exite were partly based on his reconstruction of the exite of *Cryptolithus* (1972, pp. 87-89, fig. 2). This reconstruction was modified without comment by Bergström (1973, fig. 15), and a quite different reconstruction is given by Campbell (1975, pp. 68-69, fig. 13). Dr. Campbell informs me (pers. comm.) that his figure 13 is a ventral view, and it is much more like the original of Raymond (1920, fig. 20) than are Bergström's reconstructions. Campbell used his reconstruction in the interpretation of burrows attributed to *Cryptolithus*, remarking that certain striations 'must have been produced by the ends of the exites that moved so as to shift sediment backwards and inwards towards the midline' (Campbell 1975, p. 70). Subsequently Campbell (1975, p. 81) explains that it is the ends of the lateral filaments of the branch that he considered were used to assist in digging, while more proximal filaments were used in respiration and to trap food particles. These ideas require that the exite shaft could be rotated about its axis to bring the filaments into a vertical position between the walking legs (Campbell 1975, fig. 14), and that the shaft could be flexed back and forth to sweep sediment



TEXT-FIG. 7. Diagram to explain the attitude in which appendages were buried on the right side of G.S.C. 34694. Two successive right appendages are shown, the posterior surface of coxa and leg branch towards observer and imbricated subparallel to the bedding, the gill branch projecting up towards the observer. View slightly postero-oblique to vertical, bedding plane shown tilted down away from observer, at acute angle to surface of page. Filaments of gill branches projecting upwards at slightly different angles. Compression vertical to the bedding plane, accompanying compaction, would result in the appearance shown by appendages 6 and 9 respectively of 34694 (text-fig. 5; Pl. 20, figs. 1-4). The gill branch appears short (exs.) compared to 34695, the lamellae directed strongly outwards, and, depending on the exact attitude prior to burial, the gill branch may lie partly in front of (appendages 6-9 of 34694), or on and behind the leg branch (appendages 11-13).

particles. Yet if Campbell's reconstruction (1975, fig. 13) is accepted, and the filaments were stiff enough to be used in excavation of a burrow, the overlap of one exite over that following, is too great to allow the filaments to be swung down past each other to a vertical position. A critical reinvestigation of the appendages of *Cryptolithus* is needed before there can be further discussion of function, for Campbell's suggestions seem open to question, particularly the assumption that exite filaments were used in excavation of a burrow. The recent reinvestigation of the Devonian *Phacops* (Stürmer and Bergström 1973) shows little of the outer appendage branch. It appears that, in genera other than *Olenoides*, the morphology and attitude of the outer branch is so poorly known that speculation on function is hazardous.

Function of coxa and inner branch. The inner, dorsal portion of the coxa is not preserved in any specimen, and traces of the ventral cuticle were found in only one example. The implication is that this cuticle was thin and little sclerotized, in contrast to that of the major portion of the coxa and



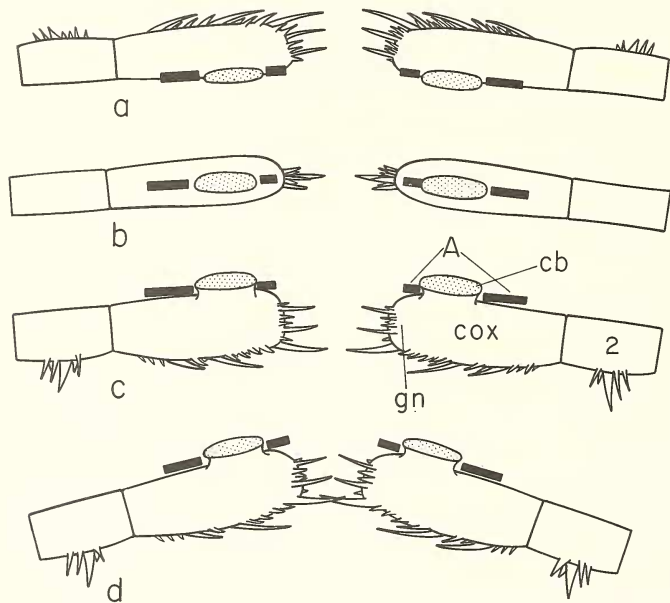
TEXT-FIG. 8. Diagram to explain the attitude in which appendages were buried in G.S.C. 34695. Two successive right appendages are shown, the gill branch lying (ventral surface visible to observer) parallel to the bedding, the posterior surface of the coxa and curved leg branch towards observer, inclined upwards and slightly forwards relative to the bedding plane. Oblique view, bedding plane outlined. The gill branch of the farther appendage is completely concealed beneath that of the nearer limb. Compression vertical to the bedding plane, accompanying compaction, would result in the appearance shown by appendages 1 and 2 of 34695 (text-fig. 6; Pl. 22, figs. 1, 2). In this specimen, preparation of gill branch 1 has revealed the complete medial and distal filaments which would have been concealed beneath portions of appendages 2 and 3.

the leg branch. The coxa appears to have been joined to the ventral cuticle adaxially (text-figs. 7, 8; cf. Whittington 1975, p. 129). Because of the thinness of the cuticle at the junction, an appropriate arrangement of extrinsic coxal muscles may have allowed considerable freedom of movement, but these movements would have been weak (cf. Manton 1977, p. 52). The specimens afford no evidence of a heavily sclerotized ventral cuticle, to which the coxa was articulated at a joint.

At the junctions between podomeres of the inner branch (Whittington 1975, p. 123, fig. 29), the dorsal margin is not sharply stepped, though interrupted at the podomere 5-6 junction by a small spine (legs 6 and 7, text-fig. 5; Pl. 20, figs. 2, 4; Pl. 21, fig. 1). The ventral margins between coxa and podomere 2, and podomeres 2 and 3, are also at the same level. These joints may have been pivot joints (Manton 1977, fig. 2.2d; text-fig. 10), that is, may have allowed movement up and down. The S-shaped curvature of the limb seen in 34695 (text-fig. 6) and other examples, implies a slight upward bend of the proximal portion of the branch, such as hinge joints would have made possible. The ventral margin at the articulations between podomeres 3-4, 4-5, 5-6, and 6-7 shows a step, with spines projecting from the step between each of the latter three articulations. There was probably a hinge joint (Manton 1977, fig. 2.2e; text-fig. 10) at the dorsal edge. Thus the coxa and leg branch could have been flexed into a curve subtending 180° or more, or extended straight or slightly upwards, only in the axial plane of the antero-posteriorly flattened limb. Overlapping rows of large and small spines are seen on the ventral and inner (gnathobasic) margins of coxae 6, 8, 12, and 13 of 34694 (Pl. 21, figs. 2, 3), and main and smaller spines on the ventral side of podomeres 2 and 3, and smaller spines at the junctions of more distal podomeres (Pl. 20, figs. 2, 4). This armature extended from the anterior (Whittington 1975, pl. 7, figs. 1-4; fig. 10) to the posterior (Pl. 21, fig. 3) appendages of the complete series, so that *O. serratus* could have used the entire series of limbs to seize and hold prey or decayed material. A median groove, flanked by the gnathobases, extended from the mid-length of the pygidium forwards to the mouth. The manner by which soft

food was squeezed, shredded, and passed forwards to the mouth by the pairs of gnathobases was described previously (Whittington 1975, p. 133). Text-fig. 9 is an attempt to show this action of a pair of gnathobases, and probable similar movements in *Triarthrus* have been advocated by Manton (1977, pp. 52-53).

The specimens do not show the original position on the body of the relatively small coxa-body junction, but it seems reasonable to assume that it was approximately as shown in text-fig. 10 (cf. Whittington 1975, figs. 25, 26), i.e. each pair of gnathobases was relatively closely opposed (text-fig. 9). The principal movement of the coxa and leg branch was a promotor-remotor swing about an approximately transverse axis through the coxa-body junction. This swing of the series



TEXT-FIG. 9. Diagrams in dorsal view of the coxa and podomere 2 of a pair of leg branches, showing the results of movements at the coxa-body junction. An axis of swing (A) at the junction is shown as a solid black bar, the axis in *a*, *b*, *c*, directed outwards and slightly backwards at 5° to the transverse plane. *a*, at limit of promotor swing, coxa and podomere 2 in oblique anterodorsal aspect, maximum separation between gnathobases. *b*, coxa and podomere 2 vertical, in dorsal aspect. *c*, at limit of remotor swing, coxa and podomere 2 in oblique postero-dorsal aspect, gnathobases at closest approach. Coxa-body junction stippled. The limb at the limit of the remotor swing (*c*) is at a greater angle to the transverse, vertical plane than the limb at the limit of the promotor swing (*a*). *d*, as (*c*), but with a slight adduction of the coxae and a twist at the coxa-body junction (clockwise on the right, anticlockwise on the left) so that the axis of swing is inclined at about 15° to the transverse plane. The effect is to bring the gnathobases closer together and slightly forward of the position in (*c*).

of limbs in a metachronal rhythm in walking, is discussed in the succeeding section. In text-fig. 9a-c, it is suggested that the axis of swing was directed outwards and slightly backwards, and the effect is that the gnathobases are closest at the end of the remotor swing, and move further apart during the promotor swing. Thus food could be squeezed and released to the next pair of coxae in front, and so passed forwards to the mouth. This effect could have been aided by slight adduction of the coxae combined with a slight twist of the axis at the end of the backstroke (text-fig. 9d). Such movements could have been made possible by appropriate extrinsic musculature, because the coxa was joined to the flexible ventral cuticle of the body. This junction having been relatively small and not rigid, these movements would have been adequate for squeezing and shredding soft food and passing it forwards, but would not have provided a strong biting and crushing mechanism.

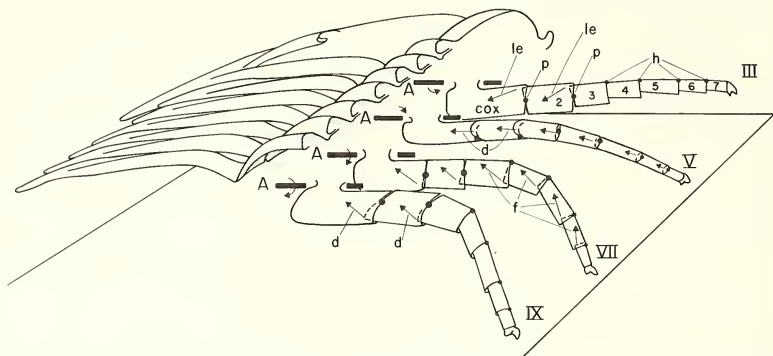
The distal podomere (7) of each leg branch is the shortest, and does not taper (Pl. 21, fig. 1; Pl. 22, figs. 1, 2; see also Whittington 1975, pl. 5, fig. 1; pl. 7, figs. 1, 3; pl. 18, fig. 2; pl. 24, fig. 4). Into the tip are inserted three spines, a large median and two lateral, each bluntly tapering, with the tip a sharp point. These spines are preserved turned inwards, in lateral view in 34694 (text-fig. 5; Pl. 21, fig. 1); in ventral aspect, extended, in 34695 (text-fig. 6; Pl. 22, figs. 1, 2). Presumably they were movable; there was ample space in podomere 7 for muscles attached to them, and they were an aid to digging when the limb was flexed.

The morphology of the coxa and leg branch is consistent, therefore, with *O. serratus* having been a benthonic predator, able to dig in search of prey, as well as for concealment. The activities by which it hunted for food are considered in the next section.

THE ACTIVITY OF *OLENOIDES SERRATUS* AND POSSIBLE RESULTANT TRACE FOSSILS

Walking. The basic limb movements employed in walking by Recent arthropods in which the leg is longer than the sagittal length of the segment, are explained by Manton (1977, pp. 39-49). The suggested manner in which *O. serratus* walked (Whittington 1975, pp. 129-131, figs. 25-28) was based on this work. Text-fig. 10 is an attempt to clarify the action of the coxa and leg branch in such walking, by showing four stages in the promotor-remotor swing, about an approximately horizontal, transverse axis at the coxa-body junction. The action of supposed intrinsic leg muscles is shown, in varying the length of the leg, keeping the tip firmly on the substrate, and giving the propulsive force. The muscles extrinsic to the coxa, which effected the promotor-remotor swing, are not shown. Each pair of legs moved in unison, and it is essential for effective walking that the tip of the limb be kept firmly in one spot during the remotor swing. It is because of this that the length of the leg, as measured in a straight line from axis of swing to tip of limb (Manton 1977, fig. 2.3), changes during the remotor swing, the leg extending (text-fig. 10, limb V) as the tip is put down, flexing (text-fig. 10, limb VII) as it moves into the vertical plane through the axis, and extending (text-fig. 10, limb IX) as the limb swings back behind this plane. There may have been eight legs in each metachronal wave of movement, legs V-IX in text-fig. 10 (in which legs VI and VIII are omitted) propulsive on the sea bottom, legs II-IV in text-fig. 10 (in which legs II and IV are omitted) swinging forwards in the recovery phase. A series of 'stills' in this gait are depicted in text-fig. 11, together with their relation to the trackway. The body is well supported in this slow movement close to the ground, each leg in a curve convex upwards which gives a hanging stance (Manton 1977, p. 200, fig. 5.1). In *O. serratus*, legs III to XI are of similar size, legs I, II, XII-XV being shorter. Thus the track made in this gait (text-fig. 11 and Whittington 1975, fig. 28) consists of a parallel series of overlapping footprints of legs III to XI, with footprints of legs I, II, XII, and XIII slightly closer to the midline. In text-fig. 11 the imprints of legs XIV and XV, which would have been successively slightly closer to the midline than those of legs XII and XIII, are not shown for simplicity; in such gaits the shorter limbs may not always make contact with the bottom. If the gait had been slightly different, for example in the phase difference between successive leg movements, or in the duration of forward and back strokes, the number of legs in a metachronal

wave would have been different, but the track would remain essentially similar. That is, it would consist of two parallel overlapping series of prints, and at intervals, a pattern of imprints inside the parallel series. Only the nature of the inside pattern would vary slightly with small changes in gait. It will be appreciated that the neat, round footprints of text-fig. 11 are idealized; when walking in soft sediment the print would have been less neat, and may have been elaborated with additional lines, curved forwards and outwards, as the tip of the limb was withdrawn and swung forwards.



TEXT-FIG. 10. Oblique diagram of *Olenoides serratus* to show promotor-remotor swing of coxa and leg branch in walking, together with supposed joints between podomeres and action of intrinsic muscles. Right coxa and leg branch III, V, VII, and IX are shown, in positions corresponding to those in text-fig. 11c. Limb III has been lifted off the ground by levator muscles, extended by hydrostatic pressure, and is half-way through the promotor swing about axis A. Limb V, extended at the beginning of the remotor swing, has tip of limb held firmly on sediment by action of depressor muscles on podomeres 2 and 3, and action of flexor muscles on podomeres 4-7 gives propulsive force to body. Limb VII has reached mid-point of remotor swing, and lies in the vertical transverse plane through the axis of swing (A). Action of flexor muscles has given propulsive force and flexed leg to accommodate to reduced length, depressor muscles have kept tip of limb firmly on sediment. Limb IX is extended at the end of the remotor swing, the depressor muscles have given the propulsive force and kept tip of the limb on the sediment, the flexor muscles relax and allow podomeres 4-7 to become aligned and extend the limb. Black circles show position of joints; dashed lines show portion of podomere which inserts into coxa or podomere proximal to it; curved arrows show amount of rotation about axis; straight arrows show direction of pull of muscles.

Seilacher (1955, text-fig. 1b, c, d) illustrated what he regarded as forward walking tracks of trilobites, and offered an interpretation (1955, p. 346, text-fig. 1a) of how they were made. It requires that the pairs of legs be longest anteriorly, diminishing in length progressively backwards, that only the anterior seven to nine pairs of limbs were used in walking, and that the pairs moved in opposite phase. In *O. serratus* (text-figs. 9-11) it is here assumed that the promotor-remotor swing of a pair of limbs in unison was used in walking and to macerate food and carry it forwards to the mouth. Dr. S. M. Manton pointed out (pers. comm.) that only for special reasons in certain groups of Recent arthropods is a pair of legs moved sometimes in the same phase, and at other times in an opposite manner. Thus I regard Seilacher's interpretation as inherently an unlikely manner of walking for any trilobite. It is possible, however, that the tracks, illustrated by Seilacher (1955, pl. 16, fig. 3; text-fig. 1b, c, d) were made by an arthropod walking in the manner here

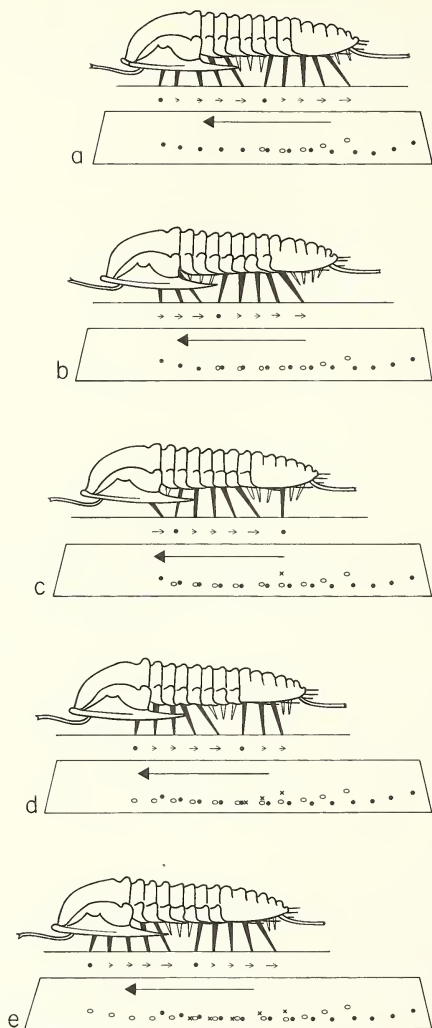
suggested, the outward and forwardly directed impressions being made as the limbs were withdrawn. This possibility requires further investigation. Seilacher (1955, text-fig. 1*e,f*) used the manner of walking he proposed in the interpretation of another track as that of oblique walking. In this he has been followed by Osgood (1970, p. 352, text-figs. 17*b*, 20*a*, etc.). Such tracks should be re-examined, and the interpretation reassessed.

A different Lower Cambrian track was regarded by Seilacher (1959, pp. 390–391, fig. 2*b*) as made by a trilobite walking forwards. It consists of a closely spaced repetition of eleven or twelve paired imprints arranged in a 'V' opening forwards, and having a pair of grooves between the imprints at the base of the 'V' (the left half is shown in the text-fig. 12). Seilacher suggested that eleven or twelve pairs of limbs only were used in walking, the series moving in a single metachronal wave at one time. Text-fig. 12 is an attempt to fit this manner of progress to the track, using the trilobite drawn by Seilacher. The appearance is improbably unstable, and Dr. S. M. Manton informed me (pers. comm.) that she knew of no Recent arthropod that when walking had one metachronal wave of limb movement upon the limb series at one time. In locomotory mechanisms considered by Manton (1977, pp. 293–331) every device is used to keep the number of supporting legs as even as possible, i.e. to keep the load on each leg similar (cf. text-fig. 11). I conclude that the way in which this track was made requires reassessment.

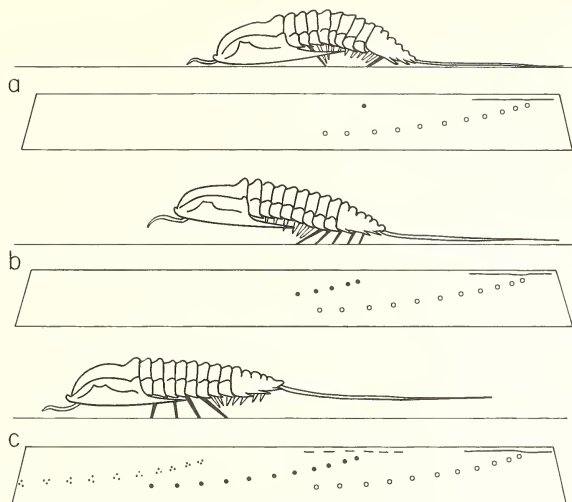
The further suggestion (Seilacher 1939, p. 391; Osgood 1970, pp. 351–352; 1975, p. 98) that in rapid walking only the longer, stronger, anterior legs of a trilobite were used, and that the hinder portion of the animal was supported, sliding along on the cerci or pygidial border spines, is also improbable. At any speed of walking, dragging part of the body is a hindrance, and the speed of walking does not depend on the supposed strength of longer legs, but on the pattern of the gait (Manton 1977, pp. 298–308). The lateral bristles on the cerci of *O. serratus* (Pl. 21, fig. 1) do not suggest that the cerci were adapted to slide on.

Jumping off the sea bottom. An undescribed trace fossil, showing a series of paired imprints repeated at intervals, led Manton (1977, p. 48) to refer to the possibility of a trilobite using a few successive limb pairs to launch itself off the bottom and drift or swim before sinking down again. Text-fig. 13 shows this activity of the thoracic limbs (which are similar in length), and the resulting tracks. In the back stroke the limb movements are not synchronous, but in a wave with a slight phase difference between each successive leg. Thus limb pair X end the backstroke and are the first to leave the bottom, and pair IV are the last. On landing, pair X have completed the forward swing and touch down first, followed in rapid succession by pairs IX to IV. Pair X begin the remotor swing first, and the limbs move in succession into the positions shown in text-fig. 13*a* for the next jump. In a favourable current this appears a plausible mode of progression for *O. serratus*, which probably had feeble swimming powers. The distance between the parallel sets of paired impressions (text-fig. 13*c*) would have depended on the strength of the jump, on the swimming powers, and the direction and strength of any current; many variations on the simple pattern of text-fig. 13 may have occurred. The track shown in text-fig. 12 is a repetitive pattern, involving far more pairs of limbs than that of text-fig. 13. To fit the trilobite shown in text-fig. 12 to the track, when progressing in short jumps, is difficult, requiring not only a wide angle of swing of the legs, but also that the posterior pairs be long and steeply inclined. It does not appear a plausible interpretation of this track.

Digging and furrowing. It is reasonable to suggest that in hunting for small, mainly soft-bodied animals, and in scavenging, *O. serratus* dug into the substrate. Such digging could have been effected by flexure and extension of pairs of limbs along the body, the leg branches directed outwards, with a slight fanning anteriorly and posteriorly (text-fig. 14). The promotor–remotor swing of the limbs is not involved in this activity; at the late Dr. Manton's suggestion I portray flexure and extension of alternate pairs of limbs. The excavation so made would have been bilobed, and some of the transverse grooves dug during flexure might be visible. It is possible that if the animal dug sufficiently deeply, and if it rested in the excavation (in part for concealment), the impressions of the ventral margins of the exoskeleton, including spines, and even of the limbs themselves, might be preserved.



TEXT-FIG. 11. See explanation on p. 197.



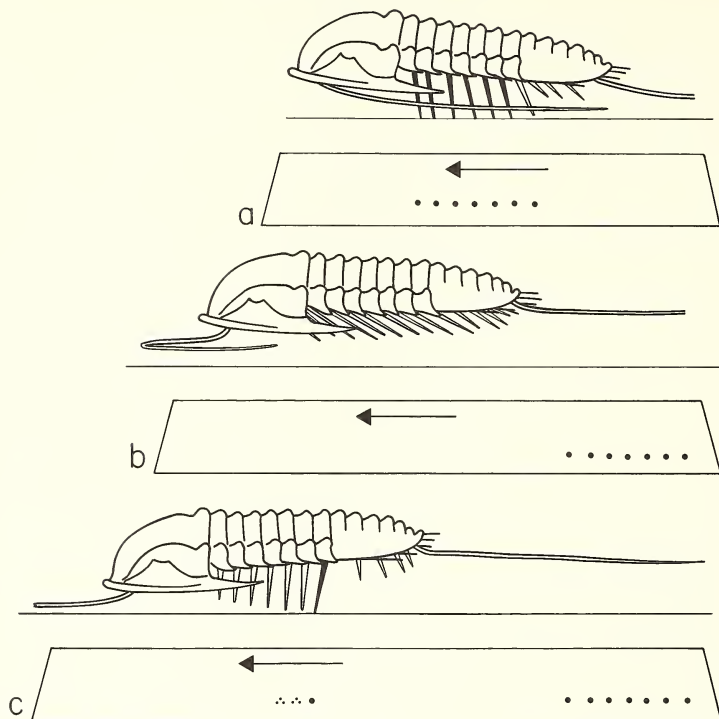
TEXT-FIG. 12. A most improbable mode of progression for a trilobite, suggested to explain a particular track.

The left half of the symmetrical track (after Seilacher 1959, fig. 2b) is shown in oblique lateral view, below each 'still' of the trilobite progressing forwards in the manner suggested by Seilacher (1959, pp. 390-391). Legs XVII to VII are supposed to have been used in successive pairs, in a single wave of motion which proceeded forwards along the body.

a, open circles show track of preceding wave, limb VII at end of remotor swing resting in anterior print of this track. Body flexed to bring limb XVII forwards to begin first print (solid circle) of next wave. Pygidium flexed down and cercus makes impression between posterior prints of preceding wave. *b*, limbs XVII to XIII are put down successively and begin remotor swing. Cercus lifts off bottom. *c*, Limbs XVII to XI complete remotor swing, lift off, and are shown in stages of promotor swing. Limbs X to VII on sea bottom, in stages of remotor swing, complete the set of impressions. Position of next set shown by stipple, which will begin as limb VII completes remotor swing and body flexes (*a*). The trilobite shown is like that depicted by Seilacher, legs in contact with sea bottom shown in solid black, those off the bottom in outline.

TEXT-FIG. 11. How a trilobite probably walked. Left lateral 'stills' of progression of *Olenoides serratus* in the possible gait described in Whittington 1975, pp. 129-131, figs. 25, 26E, 27 (cf. Manton 1977, fig. 2.5). *a-e* are successive stages, progressing in the direction shown by the large arrow, which lies in the sagittal plane. Each metachronal wave of eight leg pairs passes forwards along the body. Thirteen pairs of legs are shown being used in this gait (i.e. the last two pairs are not used). Each selected still-stand shows left legs only, in solid black when in contact with the sea bottom, in outline when off the bottom and swinging forwards. Respectively: *a*, legs I-V in first wave, VI-XIII in second wave; *b*, legs I-III in first wave, IV-XI in second wave, XII, XIII in third wave. *c*, leg I in first wave, legs II-IX in second wave (legs II and III are off the bottom and concealed beneath the cephalon), legs X-XIII continuing the third wave; *d*, legs I-VII (legs I and II concealed) in second wave, VIII-XIII in third wave; *e*, legs I-V in second wave, VI-XIII in third wave. Below tip of each limb on bottom is either a solid circle, showing limb tip has just been put down, or an arrow of length proportional to amount of backstroke completed. The panel below each 'still' shows in oblique lateral view the left half of the symmetrical track made in this gait, solid circles are footfalls of first wave affecting legs I-V in *a*, open circles footfalls of second wave, crosses (*c*, *d*, *e*) footfalls of third wave.

Antenna and cercus incomplete.

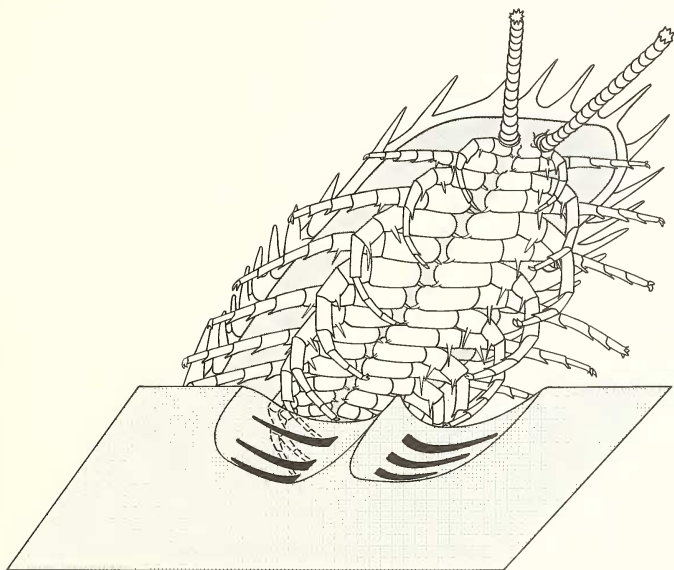


TEXT-FIG. 13. Left lateral 'stills' of how *Olenoides serratus* may have launched itself off the sea bottom to drift or swim a short distance before descending to the bottom (cf. Manton 1977, p. 48). *a*, leg pairs IV to X swung back quickly launches animal, imprint of left legs shown in oblique lateral view in panel below. *b*, animal drifts or swims, pairs of legs swung back to offer less resistance. *c*, leg pairs IV-X in promotor swing, pair X complete swing and touch bottom, to be followed in succession by pairs IX to IV, giving a second set of impressions. Antenna incomplete, cercus complete in *c*. Limbs in solid black in contact with sea bottom, arrow in sagittal plane of animal shows direction of movement.

Such traces have long been known as *Rusophycus* (Crimes 1970 and references; Osgood 1970, pp. 301-308), and Crimes (1975) and Baldwin (1977) have argued that these excavations were cast in sand or silt at the sediment-water interface. Not all bilobed excavations were the work of trilobites (e.g. Osgood 1970, pp. 303-304), but those showing impressions of the exoskeleton or of limbs, appear indubitably so. Osgood (1970, p. 304, pl. 57, fig. 6; pl. 58, figs. 4, 5) also refers to three specimens of *Rusophycus*, in one of which the exoskeleton of the trilobite *Flexicalymene meeki* lies upon the cast of an excavation. He regards the specimens as proving that the excavation was

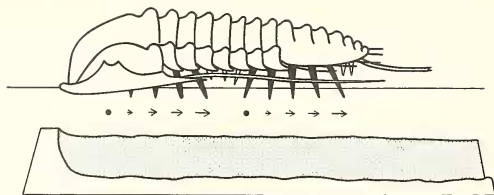
made by a trilobite. However, if one accepts the explanation by Crimes (1975, pp. 41–47) that the excavation was dug and subsequently cast in sand or silt, I have difficulty in understanding how the exoskeleton comes to lie 'in place' above the cast. Despite the doubts and difficulties in interpreting specimens of *Rusophycus*, it does appear possible that digging by *O. serratus* in search of prey or for concealment (text-fig. 14), could have resulted in a *Rusophycus* type of trace. Indeed, both Martinsson (1965, p. 211) and Bergström (1973, p. 54) have argued that such traces were made in hunting.

It may also be reasonable to suggest (cf. Manton 1977, p. 48) that *O. serratus* could have ploughed shallowly in loose, wet sediment in search of food. This could have been achieved using the normal walk (text-fig. 11), but with the cephalon inclined downwards and presumably the antennae swung back outside the limbs (text-fig. 15). Such an activity would have produced a shallow furrow approximating to the width of the cephalon. The footfalls would have been at the margin of the furrow, and hardly likely to be preserved in wet sediment which may have slipped at the edge of the furrow. Such a nondescript trace would not attract attention. A different type of furrow, however,



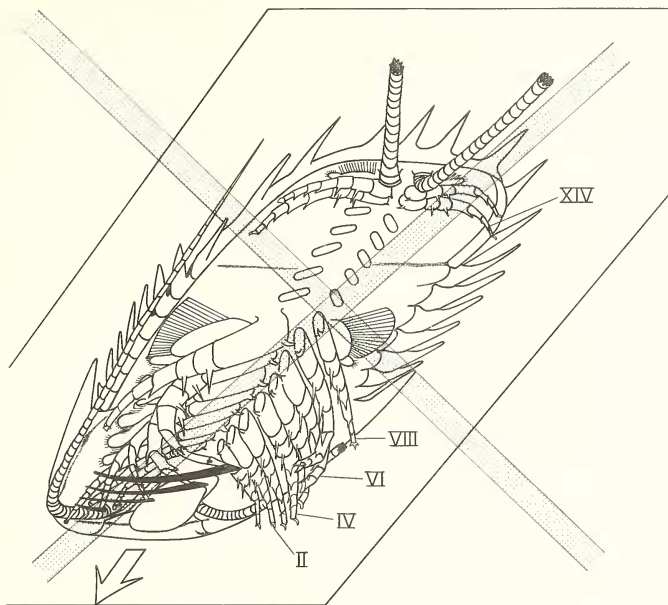
TEXT-FIG. 14. Diagrammatic oblique ventral 'still' of *Olenoides serratus* alternately flexing and extending pairs of limbs. Coxae and leg branches I to XV and their major ventral spines are shown, gill branches omitted. During flexure the limbs dug into the sediment and excavated a shallow depression. Lower part of drawing shows surface of sediment (stippled) from below, including that part of the bilobed excavation below the first seven pairs of appendages. The grooves in the excavation made by the flexure of limb pairs I, III, and V are shown in black and on the left side dashed lines show the concealed distal portions of these limbs.

Antennae assumed to be forwardly extended, cerci incomplete. Ventral cuticle stippled.



TEXT-FIG. 15. Left lateral 'still' of *Olenoides serratus* in gait shown in text-fig. 11, but with cephalon inclined downwards and ploughing shallowly into sediment. Horizontal line shows position of sediment surface, antennae curved back, left half of furrow shown in oblique lateral view in panel below. Other symbols as text-fig. 11.

has long been remarked upon. This is the trace fossil *Cruziana*, which has been interpreted confidently as resulting from the activity of trilobites (e.g. Seilacher 1970; Crimes 1970, 1975; Birkenmajer and Bruton 1971). This trail, observed extending straight or slightly curved for a metre or more, is a bilobed furrow reaching 5–6 cm in width, each furrow showing diagonal grooves forming a V-pattern, and it has been widely agreed that the grooves diverge forwards. If such a trail was made by *O. serratus*, it should be possible to propose appropriate limb movements by which it was made, and to give a reason for this activity; I have found it impossible to do either in a plausible manner. To take limb movements first: in contrast to those shown in text-fig. 14, these movements would have to have provided forward propulsion of the animal, combined with diagonal digging. Without serious thought, I earlier (1975, p. 131) suggested that in *O. serratus* a combination of a remotor swing of the limb with flexure would give diagonal scratches. The previous section has shown that flexure of the limb was confined within the antero-posteriorly flattened plane of coxa and leg branch, because of the medial position of the pivot joints and the alignment of the hinge joints along the dorsal margin (text-fig. 10). To attain an inward and backward movement of the tip, the limb would have to have been flexed, and at the same time swung back about the horizontal axis (A in text-fig. 10). In such a postulated action, the intrinsic leg muscles would have acted to dig a groove, but the only forwardly propulsive force to the body would have to have come from the extrinsic muscles in the remotor swing. Given the nature of the coxa–body junction, narrow and with no articulation. I doubt that there would have been sufficient force to drive the body forwards, even if the limb series were to have been acting in metachronal waves. Text-fig. 16 shows movements of limbs in pairs which could have dug grooves directed inwards and backwards, and may at the same time have given a variable and uneven drag forwards to the animal. If each limb was swung at the coxa–body junction, about a vertical axis, into an outward and forward-directed position, then as the leg flexed it would have dug a groove inwards. The limb is suggested to have been directed in this manner, in order that if there were resistance to digging, then the animal would have been dragged forwards as the groove was cut. Text-fig. 16 suggests that the limbs may have worked in a metachronal wave of six, and shows limb pairs III to VII in successive stages of digging a groove, with limb pair VIII extended off the ground after completing the digging action. Limb pairs I, II, XIV, and XV are shown as not taking part in the digging, and are extended above the sea bottom. The track of the groove dug by a limb is a resultant of inward digging and forward progress. If the sediment in which the animal was digging was so wet as to offer no resistance, a straight groove would have been dug, and there would have been no forward progress. If resistance were offered, the groove would have been curved, the amount of curvature determined by the resultant forward progress. If resistance varied between one side and the other, the direction of movement would have been shifted. Successive waves would have formed an over-



TEXT-FIG. 16. A highly improbable mode of progression for a trilobite. Diagrammatic oblique ventral 'still' of *Olenoides serratus*, limb pairs I to XIII swung into a forward and outward direction, pairs III to VIII in stages of a metachronal wave of flexure and extension. It is assumed that limb pairs I, II, XIV, and XV did not take part in the movement, remaining extended; limb pairs IX to XIII not shown for simplicity, gill branches lying beneath the ventral cuticle, antennae curved back beside body, cerci incomplete. As each limb was flexed it would dig a groove; these grooves are shown beneath the left side only, for simplicity. Arrow suggests direction in which animal may have been dragged forwards by digging action.

lapping series of grooves varying in direction and curvature (not symmetrical), typical characters of *Cruziana* (cf. Birkenmajer and Bruton 1971, fig. 10). A metachronal rhythm of the type suggested may have given a more or less continuous forward push, and have maintained the body in a roughly horizontal position, supported along its length. The lateral border and genal spine may have made a lateral groove, and the movement of the curved-back antenna a smoother zone inside the groove (Crimes 1975, fig. 1). The gill branches would have lain beneath the ventral cuticle (text-fig. 16), protected by the pleural regions, and could not have assisted in excavation. For this activity to have been effective, the coxa and leg branch would have to have been held at a fixed angle (45° to the sagittal line is chosen in text-fig. 16). This activity may appear plausible at first glance, but the late Dr. Manton regarded it as highly unlikely, advising me against publication of text-fig. 16 because it was so misleading. I disregard her advice with considerable hesitation, and

superimpose a cross on the figure. There are two major considerations that make this activity unlikely:

(1) as a method of seeking food it is slow, clumsy, and inefficient. With the limbs in the position shown, opposing pairs cannot have been flexed to grasp prey efficiently with the numerous spines, as they could in the *Rusophycus* type of activity (text-fig. 14). That is, if the animal had encountered a small worm or other prey, it would have had to swing the limbs outwards into the transverse plane to seize it, and also to begin the promotor-remotor movements which would have enabled it to tear up the food and convey it forwards to the mouth. Far more efficient would have been for the animal to have sought food by walking (text-fig. 11) or ploughing (text-fig. 15) shallowly over the sea bottom, and on detecting it to have dug down and seized it between the flexed limbs (text-fig. 14).

(2) Dr. S. M. Manton, who has recorded the walking trails made under water by many Recent marine arthropods, assures me that no comparable trail is known. That is, no living arthropod is known to progress forwards by such limb movements; in locomotion the tip of the limb is kept on one spot during the propulsive stroke.

I conclude that *O. serratus* did not behave in the manner portrayed in text-fig. 16, and can devise no plausible way by which it could have made the *Cruziana* type of trace. The arguments by which *Cruziana* is attributed to trilobites (e.g. Seilacher 1970, pp. 448-449) are not conclusive, and discussions of how the trace was made (e.g. Birkenmajer and Bruton 1970, pp. 313-317; Crimes 1970, pp. 51, 61-65; 1975, pp. 36-37; Seilacher 1970, pp. 449-452) are vague and unsatisfactory, particularly in not explaining how forward progression combined with excavation was accomplished. The origin of this trace is an unsolved problem, as is the question of any relationship between the *Cruziana* and *Rusophycus* types of traces. In the Middle Cambrian Burgess Shale fauna, kinds of non-trilobite arthropods outnumber trilobites by at least two to one. Perhaps the *Cruziana* trace was made by a non-trilobite arthropod, or even by some animal other than an arthropod.

Sideways raking. Traces which include groups of parallel scratches have been attributed to trilobites (Osgood 1975, pp. 98-100, and references). These include the celebrated sideways raking described by Seilacher (1955, pp. 349-355, pl. 17, fig. 2, text-fig. 3), in which the activity of the appendages in making the track is portrayed. The legs of one side are shown as flexing and extending, in a wave of motion which moved forwards along the body, while the tips of the extended legs of the other side acted as rakes as the animal moved sideways. This appears at first glance as a plausible activity for *O. serratus* (cf. Whittington 1975, p. 131, fig. 29). Seilacher interpreted the raking activity as for feeding, systematically stirring up food particles, which were filtered by the gill branches and carried to the mouth by currents resulting from the limb movements. I consider this mechanism for food transport as improbable, and regard *O. serratus* as not a filter feeder. Sideways raking as a method of hunting seems less efficient than walking or shallow ploughing, and thus an unlikely activity for *O. serratus*. Other criticisms of interpretations of raking trails are mentioned by Osgood (1975).

Activity of other trilobites. My conclusions on the mode of life of a second trilobite from the Burgess Shale, the unique *Naraoia compacta* (Whittington 1977, pp. 436-439), are like those on *O. serratus*, as modified and expanded here. *N. compacta* possessed an exceptionally powerful apparatus for seizing and macerating food, and the single articulation in the thorax was apparently an adaptation well suited to shallow ploughing of the type shown in text-fig. 15. Most probably it behaved much as *O. serratus* may have done (text-figs. 11, 13, 14) in walking, jumping, and drifting, and in digging, but I now regard sideways raking as unlikely and the making of the *Cruziana*-like furrow as an improbable activity for *N. compacta*.

Appendages are also known in one species each of *Ceraurus* (Störmer 1939, 1951), *Phacops* (Seilacher 1962; Störmer and Bergström 1973), *Triarthrus* (Cisne 1975), and *Cryptolithus* (Campbell 1975, fig. 13), which range in age from Ordovician to Devonian. In each, the series of limbs is graded in length, shorter anteriorly, of similar length from the last somite of the cephalon to

posteriorly in the thorax, then a rapid diminution in the pygidium. I consider that the manner of walking in all these species was like that in text-fig. 11 (resulting in a track of that type), and not like either of the ways suggested by Seilacher (1955, fig. 1a; 1959, fig. 2b and text-fig. 12). The interpretation of certain tracks by Seilacher (1955) and Osgood (1970) therefore requires re-examination. I consider it unlikely that trilobites normally walked using only a few anterior pairs of limbs, and that the pygidium was dragged along. These species have all been interpreted as filter feeders, except *Phacops* (Stürmer and Bergström 1973, pp. 118–120), considered both a predator and filter feeder. I am not persuaded by the arguments advanced for filter feeding, but if this were the habit, then presumably sideways raking was a possible activity. Shallow ploughing (text-fig. 15), jumping and drifting (text-fig. 13), and digging (text-fig. 14) for concealment if not in hunting, are likely activities. For the reasons given in the previous section, I am doubtful that *Cruziana* should be attributed to trilobites, so that text-fig. 16 represents a most unlikely activity for any of these species.

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